

A Learning Model for L/M Specificity in Ganglion Cells

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Outline

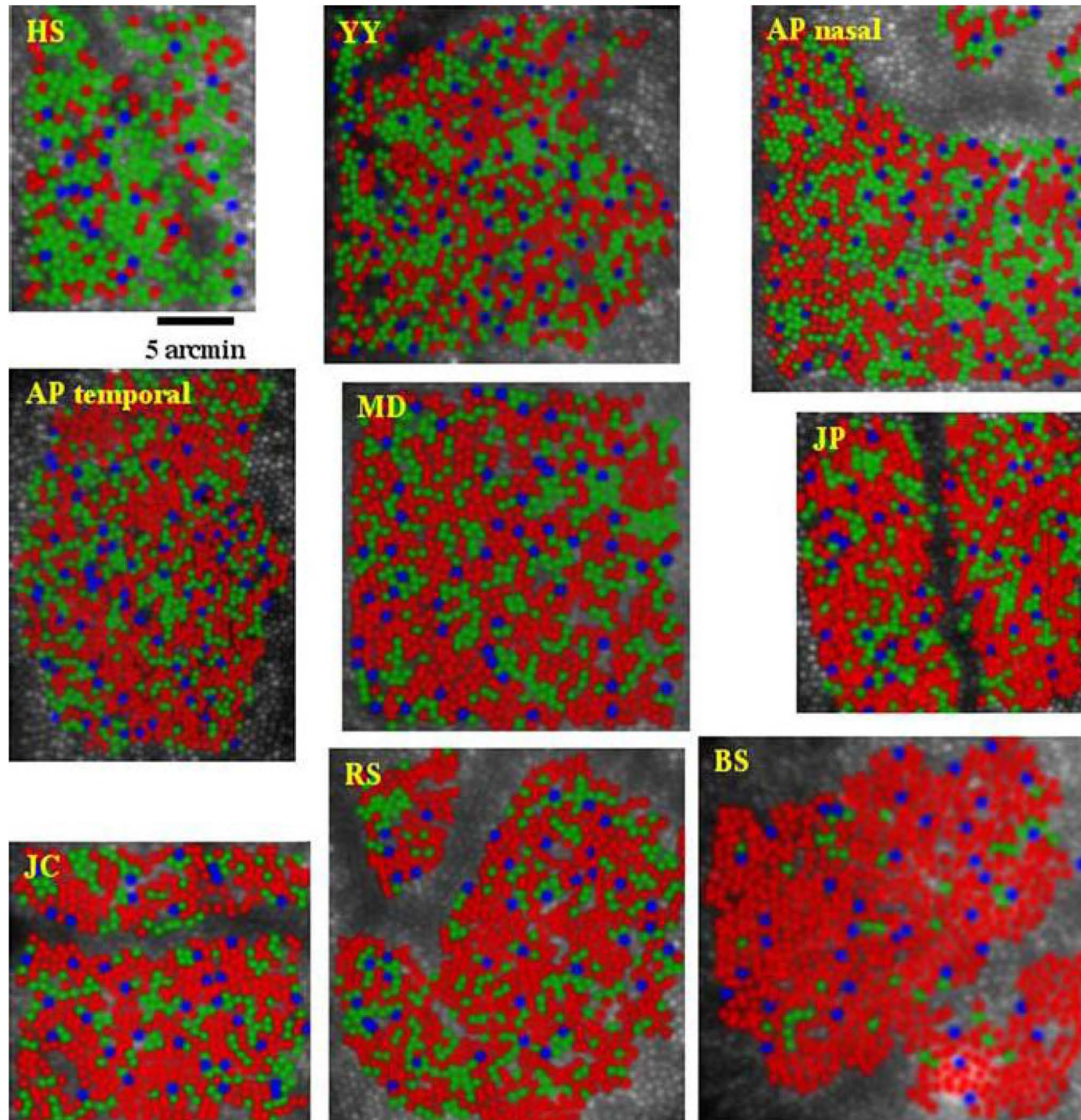
Review the cone-indiscriminate wiring model for ganglion cells.

Describe the resulting signal-to-noise issue.

Show how associative learning in the retina could generate cone-specific ganglion cells.

Discuss some implications.

Hofer, Carroll, Neitz, Neitz & Williams (2005) JNS



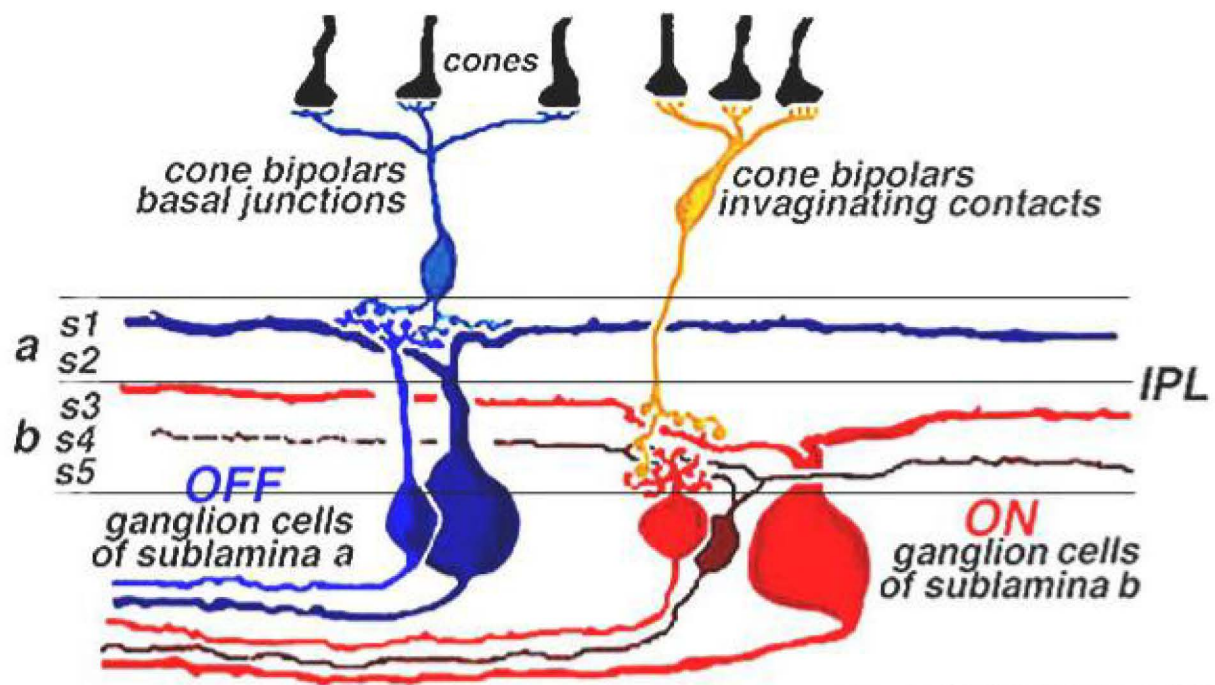
L/M Cone Array Model

Spatially random array of cones with a proportion p_L of L cones and $p_M = 1 - p_L$ of M cones.

$c_{L,i}$ is the signal from L cone i ;

$c_{M,j}$ is the signal from M cone j .

Retinal Ganglion Cells



Nelson, Famiglietti & Kolb, 1978

Ganglion Cell Model

g_L , output of an L-center ganglion cell

$$g_L = c_{L,0} - \left(\sum_i w_{L,i} c_{L,i} + \sum_j w_{M,j} c_{M,j} \right)$$

$$w_{L,i}, w_{M,j} \geq 0$$

$$\begin{aligned} W_T &= W_L + W_M \\ &= \sum_i w_{L,i} + \sum_j w_{M,j} \leq 1 \end{aligned}$$

A balanced cell is color pure for a uniform stimulus .

Paulus & Kröger-Paulus (1983 VR).

“A new concept of retinal colour coding.”

$$g_L = c_{L,0} - \left(\sum_i w_{L,i} c_{L,i} + \sum_j w_{M,j} c_{M,j} \right)$$

$$g_L = L - \left(\sum_i w_{L,i} L + \sum_j w_{M,i} M \right)$$

$$= L(1 - W_L) - M W_M$$

$$= L(1 - W_T + W_M) - M W_M$$

$$= W_M (L - M), \text{ if } W_T = 1.$$

Cone Noise Effects

Suppose we add to cone i an independent noise e_i with $E[e_i] = 0$ and $E[e_i^2] = \sigma_C^2$.

If there are N surround cones with N_M M cones, and $w_{L,i}, w_{M,j} = 1/N$,

$$W_M = N_M/N.$$

The signal to noise ratio, $s/n = E[g_L] / \text{std}[g_L]$

$$s/n = ((L-M) N_M/N) / (\sigma_C \sqrt{1+1/N})$$

Cone-specific Case

If we delete the connections from the same type of cone, and there is at least one cone of the opposite type, the signal to noise ratio is that when $N = N_M$

$$s/n = (L-M) / (\sigma_C \sqrt{1+1/N_M})$$

The ratio of the signal-to-noise ratio for the indiscriminate case to that of the cone specific case is

$$N_M(N_M+1) / (N(N+1))$$

Loss Ratio Table

$$N = 6, p_L = 2/3$$

ratio	2/42	6/42	12/42	20/42	30/42	42/42
dB	-26	-17	-11	-6	-3	0
Prob	0.18	0.25	0.22	0.16	0.10	0.03

Prob all surrounds same as center = 0.06

Average loss = -13 dB

Goals

Review the cone-indiscriminate wiring model for ganglion cells and describe its signal-to-noise problem.

- ➔ Show how associative learning in the retina could generate cone-specific ganglion cells.

Discuss some implications.

Cone Images for Training

The cones are presented with a sequence of training images that provide each of the cone types in each position a series of values.

The average behavior of the learning process depends on certain average properties of the images.

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Cone Images for Training

Simplifying assumptions:

The inputs are locally uniform,

$$c_{L,i} = L, c_{M,j} = M.$$

The average over images of the cone inputs squared is

$$E[L^2] = E[M^2] = \sigma^2.$$

The average cross correlation is

$$E[L M] = \rho \sigma^2$$

Hebbian Learning Rule

$x = (x_i)$ = a list of random variables with covariance matrix $C = (c_{i,j}) = (E[x_i x_j])$

$$y = \sum w_i x_i$$

The Hebbian associative learning rule

$$\Delta w_i = a y x_i$$

can compute the principle component of the covariance matrix, i. e. find the weights that maximize the variance of y if

$$\sum w_i^2 = 1$$

Ganglion Cell Learning Rule

$$\Delta w_{L,i}(t) = w_{L,i}(t+1) - w_{L,i}(t) = -a g(t) c_{L,i}(t)$$

Constraints: $w_i \geq 0$,

$$\sum w_i = W_L + W_M = W_T.$$

For a g_L cell, the learning rule will result in W_L going to zero if a is small enough to average out the random variations and

$$E[\sum \Delta w_{L,i} - \sum \Delta w_{M,j}] = E[\Delta W_L - \Delta W_M] < 0$$

Ganglion Cell Learning

$$\Delta w_{L,i}(t) = w_{L,i}(t+1) - w_{L,i}(t) = -a g_L(t) c_{L,i}(t)$$

For the balanced, noise-free case

$$g_L(t) = W_M(t) (L - M); \quad c_{L,i}(t) = L; \quad c_{M,i}(t) = M$$

$$E[\Delta w_{L,i}(t)] = -a W_M(t) E[L^2 - L M]$$

$$E[\Delta w_{L,i}(t)] = -a W_M(t) \sigma^2(1-\rho) \text{ [decreasing]}$$

$$E[\Delta w_{M,i}(t)] = -a W_M(t) E[L M - M^2]$$

$$E[\Delta w_{M,i}(t)] = a W_M(t) \sigma^2(1-\rho) \text{ [increasing]}$$

Ganglion Cell Learning

For the balanced, cone noise case

$$E[\Delta w_{L,i}(t)] = -a (W_M(t) \sigma^2(1-\rho) + w_{L,i}(t) \sigma_C^2)$$

$$E[\Delta w_{M,j}(t)] = a (W_M(t) \sigma^2(1-\rho) - w_{M,j}(t) \sigma_C^2)$$

Learning depends on $\sigma^2(1-\rho)$ dominating σ_C^2 .

For cones, ρ is close to 1, but for bipolars it should be small.

Finally

If L and M cells can only be distinguished by their responses to light, and if ganglion cells have cone-specific connections, learning must occur in the retina.

The CNS must have processes for pruning useless connections.

The retina could have such processes. Associative learning is a good candidate.